NOTES ON THE MORPHOLOGY OF THE GENUS LYCÆIDES (LYCÆNIDÆ, LEPIDOPTERA)[1]

By V. Nabokov

Out of the hundred or so holarctic Lycænids distributed among at least sixteen genera of the subfamily *Plebejinæ* (definitely fixed by Stempffer, 1937, Bull. soc. ent. France 42 :211, etc.; *not* covering the superficial concept of "Blues" for which no systematic term or division can exist), only fourteen species or so, two of which are obvious invaders from the Tropics, occur in the nearctic region (north of the 30th parallel). These belong to seven genera, four of which (the first four in the list given below) are holarctic and contain together six species of which one half is common to both regions. All three exclusively American genera have the free portion of the ædeagus elongated; all the exclusively palearctic genera, except *Aricia* R. L. (and the, mainly tropical, *Chilades* Moore [2] and *Freyeria* Courvoisier) have stubby or proximally "bulbous" free portions. Of the four genera common to both regions one half belongs to the first type and one half to the second.

The only *Plebejinæ*, so far known to exist in the nearctic region, are: 1. *Agriades* Hübner: *glandon* Prunner (holarctic); 2. *Vacciniina* Tutt: *optilete* Knoch (holarctic); 3. *Lycæides* Hübner: *argyrognomon* Bergsträsser (holarctic), *scudderi* Edwards, *melissa* Edwards; 4. *Plebejus* Kluk: *sæpiolus* Boisduval; 5. *Plebulina*, *n.g.* (remarkably amalgamating the *Plebejus* or *Lycæides* ædeagus with the valval *processus superior* and uncus + falces of *Albulina* Tutt): *emigdionis* Grinnell (genotype); 6. *Icaricia*, *n.g.* (allied to *Aricia* R.L. in ædeagus; somewhat to *Polyommatus* Latreille in general type of uncus as seen ventrally; close to both in *processus superior* of valve; distinguishable by the underdeveloped, *i.e.* devoid distally of any

[1] Published with the aid of a grant from the Museum of Comparative Zoölogy at Harvard College.

[2] Unexpectedly represented by *speciosa* Staudinger in the Andes.

semblance of hook, triangular, laminate, proximally very broad falx, its very gradually tapering apex hardly exceeding in height the level of its strongly humped humerulus): *icarioides* Boisduval (genotype) with its various subspecies (clamoring for a reviser) and four other species, viz.: *acmon* Doubleday-Hewitson, *sp. indeterm.* (? *chlorina* Skinner), *neurona* Skinner and *shasta* Edwards; these four structurally smaller than the genotype (with an uncus lobe distally somewhat grooved in lateral view but not actually revealing Stempffer's process as it occurs in *Aricia anteros* Freyer), and 7. *Hemiargus* Hübner: a curiously aberrant genus (somewhat allied to *Chilades* Moore) which is represented by *hanno* Stoll and in which I very provisionally retain *isola* Reakirt. An unexpected *fultura superior* is present in the former and is monstrously developed in the latter.

For some time I have been especially concerned with the genus *Lycæides*. In a preliminary paper (Nabokov, 1943 [March, 1944], Psyche **50** :87 etc.) an attempt was made to clear up several taxonomic points mainly in regard to the nearctic section; [3] the palæarctic one is still badly confused taxonomically, especially because the type specimens of a number of races have never been examined structurally (German authors, for instance, blindly relying upon the haphazard commercial identifications of the Staudinger firm). These matters I shall discuss elsewhere, but it is necessary to make a few comments regarding the genotype.

This is the "*argus* Linn." of Hübner ([1823], Verz. bekannt. Schmett. **5** :69), *nec* Linn., which was selected as the type by Scudder (1872, 4th Ann. Rep. Peabody Acad. Sci. **1871**:54; 1875, Proc. Amer. Acad. Arts Sci., Boston **10**:208), and since Hübner's *argus* is the "*Argus*" of Reverdin (1917, *in* Oberthur, Et. lép. comp. **14**:22, fig. 3, uncus) it follows that it is also the "*argyrognomon* Bergsträsser" of Tutt [and Chapman] (1909, Brit. Butt. **3**:205–208, pl. 50, fig. 2, uncus) and thus not the "*Ligurica*" of Reverdin (1917, op. cit.:22, fig. 4, uncus) which is the "*ismenias* Meigen" of Heydemann (1931, Int. ent. Zft. **25**:129) and the "*argyrognomon* Bergsträsser" of Forster (1938,

[3] With an incidental suggestion (*l.c.* : 88, *nota*) that *cleobis* Bremer falls to *subsolanus* Eversmann. I now find that Hemming (1938, Proc. R. Ent. Soc. London, **7** (1), **B** : 5–7, fig., male, type) had already come to the same conclusion.

Mitt. Munchner ent. ges. 28:11), wrongly, and belatedly, selected by the latter author as "type" with the suggestion that readers look up for themselves Hübner's plate. They do, and find (Hübner, Samml. europ. Schmett. pl. 64 [1800]) that fig. 316, to which Scudder referred when selecting the type, can be easily matched by German males of the "*Argus*" of Reverdin and of the "*argyrognomon* Bergstr." of Tutt and, consequently, of Hemming (1934, Gen. names hol. butt. 1:108), who definitely fixed it (thus excluding the other species of *Lycæides* which he knew well) as the type of the genus, and this clinches the matter, whatever the two species be called. The publication of Beuret's important paper (1935, Lambillonea 35:162, etc.) has led to attempts to transfer the name *argyrognomon* Bergsträsser (1779, Nomenclatur, 2:76–77, pl. 46, fig. 1,2) from the short-falx species (the genotype) to which it was applied by Tutt (1909) and which we shall term for the moment species X, to the long-falx species, *ismenias* Meigen, 1830 (Heydemann,[4] 1931) which we shall term species Y. These attempts have been prompted by the fact that female specimens apparently belonging to Y (Beuret, l.c., does not give the reasons for his determination), casually collected in the type locality of *argyrognomon* Bergstr., proved to be closer to Bergsträsser's equivocal figures than sympatric females of X. One cannot deny that the figures apply better to the general run of Y females than to the general run of X females; but pending further investigation, or some formal decision on the part of a special commission, I am compelled to use in this paper the name *argyrognomon* Bergstr. for X because of the following considerations: 1. As noted and illustrated by Beuret himself (1934, Lambillonea 34:119) at a time when he still called X by the name *argyrognomon*, absolute similarity to Bergsträsser's figures is exhibited by what he (inconsequently) named *argyrognomon rauraca* Beuret (*l.c.* pl. 5, 5a, fig. 9, 10. See also Beuret, 1928, Soc. Ent. 43, fig. 5, 10, uncus, *argyrognomon*, "Augst"). This, now extinct, colony was discovered on a plot of ground, a thousand feet long and 1/6 of this broad, near Augst in the Aargau, N. Switzerland, *i.e.*, some 200 miles south from the type locality (Bruchköbel Forest, in the Hesse-Nassau district, Central Germany) of *argyrognomon* Bergstr.; but mor-

[4] Whose clumsy fixation I reluctantly adopt.

phologically, *i.e.*, apart from current geographic obsessions and notwithstanding the inconvenience of the thing not flying where it ought to fly, *rauraca* Beuret was when discovered, and in my opinion remains so now, an absolute synonym of *argyrognomon argyrognomon* Bergstr., since in genitalia it corresponds to Tutt's *argyrognomon* Bergstr. and in the appearance of the female to Bergsträsser's figures; 2. There is no guarantee that the next German, or British, collector in the Hesse-Nassau district will not come across chance specimens or a little colony of X, different from the race of X (*lycidasoides* Beuret, 1934), assigned to the general region, and similar to Beuret's Aargau series — in which case the whole question would have to be brought up again (Tutt remaining the first reviser [5]); and 3. It is not at all clear what name should be used for X if "*argyrognomon*" is switched to Y. The name *acreon* Fabricius (1787 Mantissa 2:76), on the basis of a worn specimen of *argus* auct (which combined at least X and Y) in the Banksian collection was assigned to the latter omnibus species by Butler (1869, Cat. Diurn. Lep., descr. by Fabricius, in coll. B.M.: 171) which leaves us none the wiser, even if Butler did see "the type female in Copenhagen" as stated by Heydemann (1931, Int. ent. Zft. 25:150) who anyway had not seen it himself and thus was perfectly unjustified in using the name (l.c. pl. 1, fig. 4, 12) for a race of X. The name *calliopis* Boisduval ([1832] Ic. hist. lép. Europe 1:58, fig. 4,5) suggested by Hemming (1938, Proc. R. Ent. Soc. London 7,B:4) also cannot be used for X, until the female type (from Grenoble, France) and the Uriage male assigned to *calliopsis* by Oberthur (1896, Et. ent. 20, pl. 5, fig. 64) are critically investigated in the B.M. collection. In view of the fantastic misadventures which names have undergone in this genus, pedantic care must be taken, so as to avoid some new nomenclatorial trouble in the future.

The genus *Lycæides*, of which *argyrognomon* Bergstr.-Tutt is the type, is characterized by an uncus (including the falces) exceedingly different from the corresponding structure found in other subdivisions of the *Plebejinæ*, and as I think it advisable to base specific unities upon the intrageneric variation of that character which intergenerically is responsible for the greatest

[5] In the sense that by figuring the male genitalia he first applied the name *argyrognomon* Bergstr. (which previously to 1909 had covered at least two *Lycæides* species and a form of *Plebejus argus* Linn.) to a definite species.

hiatus, it is the uncus that I have selected (partly in development of Reverdin's, Chapman's, and Stempffer's views) for differentiating species in the *Lycœides.*

The male armature consists of a dorsal (in regard to the body) portion (the uncus) and of a ventral one (the valves — which have a constant fishlike shape in the *Plebejinæ*). The two are hinged to each other somewhat in the way of the lids of a shell and appear "closed" when viewed *in situ.* When teased out of the tissues and viewed ventrally, *i.e.*, when the whole organ is forced open oysterwise so that its symmetrically extended valves continue to point down, whereas the uncus lobes point distad from the observer, the most conspicuous thing about the upper portion is the presence of a pair of formidable semi-translucent hooks (the subunci or falces — of a peculiar shape not found in allied genera), produced from the opposite side of the distally twinned uncus and facing each other in the manner of the stolidly raised fists of two pugilists (of the old school) with the uncus hoods lending a Ku-Klux Klan touch to the picture. The flame-shaped distal part of the candle-shaped ædeagus reaches a point between their elbows, while its proximal part is propped by the *fultura inferior* (furca) at the root of the valves.

In the paper already referred to, I introduced the following terms: **F.** for the length of the upright portion, or *forearm*, of the falx measured from its distal point to the apex of its elbow; **H.** for the length of the *humerulus* of the falx, from the apex of its elbow to the apex of its shoulder; and **U.** for the length of the *uncus lobe* from its distal point to the apex of the shoulder of the falx. In the majority of some 500 preparations, regardless of whether the elbow of the falx happened to be raised (in the follow-through of an "uppercut," to pursue the pugilistic image) as it is for instance in fig. ARG.A. of pl. 1, or whether it remained in its normal position (*i.e.* with the forearm parallel to the axis of the uncus lobe), a rather curious fact was noticed, namely that the distance between the tip of the falx and the apex of the shoulder exactly equalled U. This suggested the tracing of a triangle, FHU, its lines joining three points: apex of forearm, apex of elbow, and apex of shoulder. A glance at fig. 1 will show that, according to the dimensions of forearm, humerulus and uncus lobe, this triangle assumes a different size (showing the gradual generic development) and a different shape (showing the specific relative dimensions of parts).

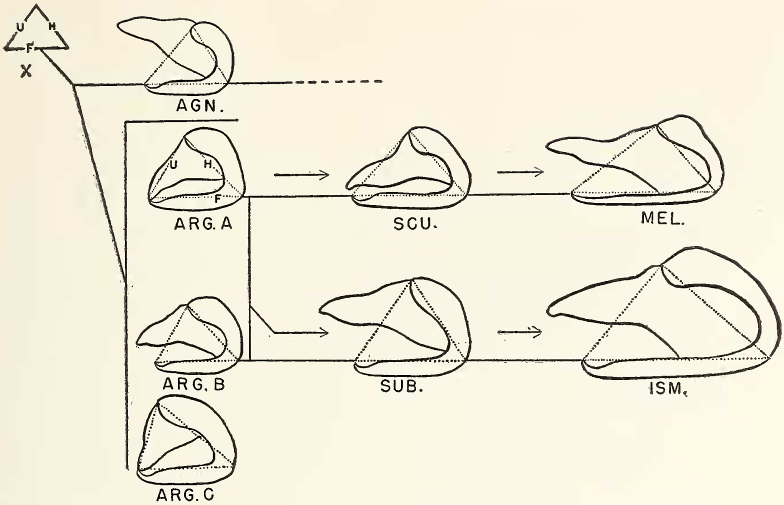


FIG. 1. EVOLUTION AND SPECIATION OF UNCUS IN LYCÆIDES
(All the figures are × 33)

F — length of forearm of falx.
H — length of humerulus of falx.
U — length of uncus lobe, equal to distance between apex of falx and apex of shoulder.
FHU — triangle for measuring relative dimensions of parts.
X — hypothetical ancestor; FHU = 0.25 + 0.22 + 0.22 = 0.69 mm.
AGN — *agnata agnata* Staudinger, prep. 193, "Maralbaschi [Maralbashi, W. Sinkiang, Central Asia]" *ex coll.* Weeks, M.C.Z.; FHU = 0.33 + 0.26 + 0.30 = 0.89 mm.
ARG.A — *argyrognomon* Bergstrasser ssp. (*ssp. anna* Edw. *prox.*), prep. 348, "Brewster, Washington [N. America], 18–VII–1940" coll. Stallings-Turner; FHU = 0.36 + 0.33 + 0.27 = 0.96 mm.
ARG.B — *argyrognomon bellieri* Oberthuz, prep. 189, "Corsica [S. Europe]" *ex coll.* Weeks, M.C.Z.; FHU = 0.33 + 0.30 + 0.25 = 0.88 mm.
ARG.C — *argyrognomon* Bengstr. ssp. (*ssp. opulenta* Verity *prox.*), prep. 211, "Alto Adigo [N. Italy] 3–VII–1930," *ex* coll. Weeks, M.C.Z.; FHU = 0.39 + 0.40 + 0.27 = 1.06 mm.
SCU — *scudderi scudderi* Edwards, prep. 168, neotype, "Saskatchewan [N. America] [*leg.*] Kennicott," M.C.Z.; FHU = 0.45 + 0.34 + 0.34 = 1.13 mm.
SUB — *subsolanus* Bremer *ssp.*, prep. 242, "Korea [E. Asia], 27–VII–1933, *leg.* Suk," M.C.Z.; FHU = 0.44 + 0.39 + 0.39 = 1.22 mm.
MEL — *melissa samuelis* Nabokov, prep. 338, holotype, "[Albany, New York] Orig. Pl. 6, fig. 6, Butt. N. Engl. Cab. S.H. Scudder," M.C.Z.; FHU = 0.57 + 0.35 + 0.44 = 1.36 mm.
ISM — *ismenias calabricola* Verity, prep. 152, "San Fili (Cosenza), Calabria [Italy] 17–VI–1920 [*leg.* fam.] Querci," *ex* coll. Weeks, M.C.Z.; FHU = 0.74 + 0.56 + 0.49 = 1.79 mm.

I view evolution in *Lycæides* as a twofold process of growth: 1. as a generic growth — involving the whole of the male genitalic structure, so that the absolute size of the uncus (independently from the size of the wings) in its general graduation from the most primitive structures (F + H + U = about 0.9 mm.) to the most specialized ones (F + H + U = about 1.8 mm.) is doubled at the maximum limit of development; and 2. as a specific growth — a process acting upon the relation of parts F, H, and U, attacking one part more strongly than the other, whereupon the latter tends to catch up with the former, producing at a certain stage stabilization and equilibrium, which eventually are again broken by unequal growth.[1] Details cannot be discussed here, but it may be noted that the generic growth produces more robust structures in the palearctic section than it does in the nearctic one; that there is also a difference in the rhythm of the specific growth (H being the part conspicuously affected in the palearctic branch, while it is the relation U/H which grows in the nearctic branch where H is more cramped and sluggish); and that throughout the general process stunted by-products occur (holarctically), reduction in absolute size of structure synchronizing here with reduction in size of wings.

I have separated the extremely numerous subspecies of which some 120, most of them badly chosen and poorly described, have names (with up to four synonyms in some cases) into six specific groups. In each there is a considerable range of racial fluctuation in the general size of the structure, and in F/U and a more limited individual fluctuation in H/U, but there is a convenient constance in the structural proportions (and in other structural details not mentioned here) of forms clustering around the main peaks of speciation. These peaks are:

agnata[6] Staudinger: small structure, with H smaller than F and slightly smaller than U;
argyrognomon Bergsträsser: small to average, with H subequal to F and greater than U;
subsolanus Eversmann: average, with H smaller than F and equal to U;
scudderi Edwards: small to average, with H still smaller than F and equal to U;

[6] It is not improbable that *agnata* produces in Turkestan a form paralleling *scudderi* (see Nabokov, l.c. : 95, *nota*).

melissa Edwards: average to large, with H much smaller than F and smaller than U;
ismenias Meigen: fairly large to very large, with H much smaller than F and greater than U.

From the arrangement on fig. 1 where selected examples of proportions are given, it will be seen that *argyrognomon*, coming from an ancestral structure from which *agnata* was also derived (and which on the basis of certain data provided by other genera I am tempted, being human, to furnish with certain characters, namely with H and U both equal to 0.2 and slightly smaller than the small F), produces two branches, which run parallel to each other in the general growth of parts. A complete sequence of intergrades (more complete than I originally thought) exists between *argyrognomon* and *scudderi* in the palearctic branch and between *argyrognomon* and *subsolanus* in the nearctic one; and I would not hesitate a moment to assign to *subsolanus* and *scudderi* a subspecific position within the polytypic *argyrognomon* had they not been centers radiating as it were their own forms and, on the other hand, had they been separated from *melissa* and *ismenias* respectively by a definite hiatus, which is not so, since racial intergrades (with a corresponding combination of pattern and structure) exist here too.

It may be added that the genus is distributed from the polar regions to just below latitude 40° in Europe and eastern North America, and to at least 30° in western North America and Asia. Its cradle is a lost country of plenty beyond the Arctic circle of today; its nurseries are the mountains of central Asia, the Alps, and the Rockies. Seldom more than two and never more than three species are known to occur in a given geographical region, and so far as records go, not more than two species have ever been seen frequenting the same puddle or the same flowery bank.

When about to draw up detailed comparative descriptions of the numerous forms, some of them new, involved in my examination of this genus, I was confronted by the fact that the pattern of the Lycænidæ had never been adequately analyzed by systematists. On the other hand, none of the works especially devoted to schemes of stripes or lines deal with that family nor can I adapt anything they contain to my needs, since pattern development and correspondence in design values are discussed by authors (Eimer, Kusnezov, Schwanwitsch, and others) from a point of view with which I entirely disagree.[7] Thus I have been forced to devise a scheme of my own.

Before passing on to this scheme, certain methodological points must be explained. An extremely exact and simple method of mapping the wing characters has been suggested by the fact that the wing is crossed by a set of concentric scale lines of equal breadth (very constantly about 0.06 mm.; sinking to 0.05 only in dwarfs and rising to 0.07 only in giants). Although a few of these lines may fork [8] here and there, their curved course is, on the whole, remarkably regular, and easily followed from costa to dorsum. By stating the meridian of the scale line and the parallel of the vein, the position of any point on the wing can be given, and by counting the scale lines occupied by a marking, the extension of the latter can be adequately measured both in its absolute size and in relation to the whole expanse of the wing. At the root of the wing the scale lines are badly blurred, since the scales here are coarse and irregular. I have thus taken for 0 the scale line crossing the wing through the base of Cu, which is especially convenient as then the axis of the forewing discoidal macule (*i.e.* the two discales or cross veins) coincides more or less with the course of the hundredth scale line (from about the 95th in average sized specimens). Out of a great number of specimens examined and measured, an average looking *Lycœides* was selected the discoidal macule of which lay exactly upon the hundredth scale line (see pl. V, the model of which was a Colorado male of *melissa melissa* Edwards, to which macules R^2 and R^3 have been added from other individuals).

When prolonged beyond the wing, the scale lines are seen to form concentric circles (the curvature of the central and distal lines, forewing, and that of the distal ones, hindwing, showing almost geometrical regularity). These, however, are not concentric with the termen (especially in the forewing) [9] and thus

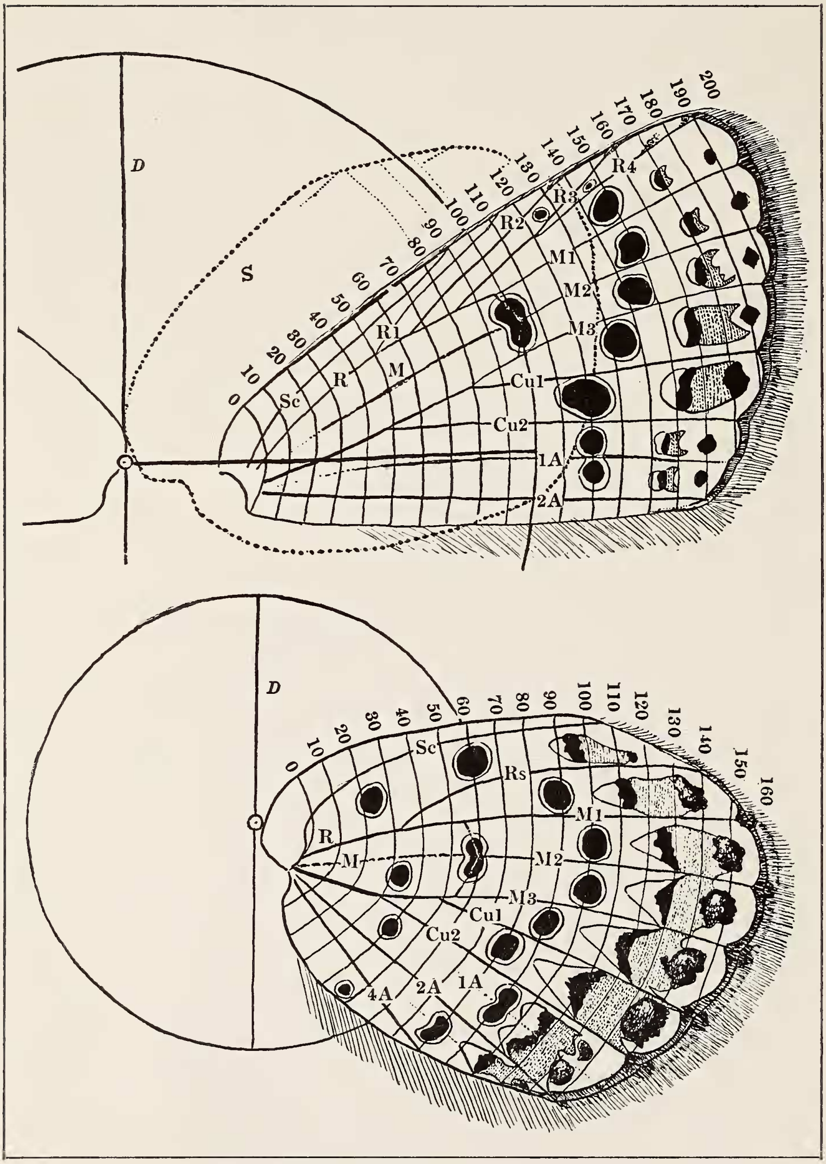
[7] While deeply enjoying the profusion of fascinating figures provided by those authors; and of course Kusnezov's masterpiece (1915, Insectes lépidoptères (Nasekomye cheshuekrylye) I (1), *in* Faune de la Russie) is unsurpassed by any other general survey of the morphology of Lepidoptera.

[8] This seems to be a more frequent occurrence in large races than in small ones, and takes place more often distally than basally but I have not yet come to any conclusion regarding the morphological value of this character.

[9] They are concentric to the termen in representatives of other subfamilies, *e.g.* in *Thecla* Fabricius (*s.s.*).

the outline of the latter seems as it were carved out (as if somebody had taken a sheet of paper that happened to be neatly ruled and had cut out a butterfly, ignoring the lines), after which the transversal disposition of the markings was more or less adapted to the new shape (especially in the case of the more distal markings) in consequence of which they ceased to follow the curvature of the scale lines. Its center in regard to the forewing lies outside the root of the latter at a point corresponding to the root of the forewing on the opposite side of the thorax, *i.e.*, at a distance from the base of the wing equal to the breadth of the body at that point; the hindwing center, however, is situated at the very root of the wing (base of costa), so that in order to make the two curvatures coincide, the right hindwing must be placed upon the right forewing in such a way as to have its hub coincide with the root of the left forewing (see plate V). My ignorance of mathematical and mechanical matters is prodigious, and thus I am quite incapable of following up certain lines of thought which these curious facts suggest.

Four veins have been lost in the course of the development of the Lycænidæ or of their ancestors. The first to go was an additional radial nervule between ScR and Rs. The next to go was 3A of hindwing. Its more recent disappearance is suggested by the rather constant reniform shape of macule 2A and by a slight halving of the cretule (*q.v.*) due to the occurrence of a line of weak scales (or a very slight scar) following the old 3A course upon a slightly darker ground. The last two veins to go were 1A and M, probably more or less simultaneously, their remnants being very similar. These remnants are: the still quite definite separation of first macule (*q.v.*) in 1A from that in Cu_2 (the oldest set), the somewhat less definite (in hindwing especially so) separation of the second macule (*q.v.*) in 1A from that in Cu_2 (a more recently evolved set) and the distinct scar of vein 1A. I have treated it as an existing vein in my classification of macules. A similar scar is visible in cell RM, the intracellular macule of the hindwing being placed *under* that scar (in other genera there is also an upper macule), and consequently I call it M. The discoidal double macule (RM) placed upon two very weak and often partly obsolescent discales, is very like macules $Cu_2 + 1A$ (the + denoting their frequent fusion). It seems likely that the third macules in Sc and Cu_2 of the hindwing travelled to their present positions distad after



Nabokov-Lycæides (× 5)

the disappearance of the veins that had once halved their cells. In the forewing the last radial is numbered R_4 since I have not come to any conclusion as to which of the initial five veins disappeared. The stalking of R_3 and R_4 seems to have occurred after the (rare and weak) first and second macules in R_3 reached their present position from a point adjacent to cell RM; their weak condition seems due to the subsequent segregation in the prison of the shortened and narrowed interspace.

An examination of all known genera of Lycænidæ, clues provided by aberrational individuals and certain ontogenetic data suggest that the maculation of a given interspace develops phylogenetically in result of a series of recurrent waves or rays of pigment, each shorter than its predecessor. An initial wedge-like or gusset-like infuscation, in the proximal corner (against cell RM) of a neutrally colored interspace, grows distad, extending along the interneural fold. This ray broadens distally; the limit (and transverse breadth) it attains varies, and this variability is responsible for the variable position and interneural breadth (filled completely in "striped" forms) of the subsequent macule. The latter is formed by a gradual deepening and concentration of the fuscous pigment at its maximal distal limit, which in the case of the *first macule* to be evolved, is subterminal. The rest of the fuscous extension is weakened, owing to this local concentration, and finally degenerates and disappears, leaving only the residue of its distal limit and the initial wedge-shaped store of fuscous in the proximal corner, whereupon the whole process is repeated (in the majority of the Lycænidæ). It is repeated with a little less vigour but with more variety in the limit of the fuscous extension and hence in the position and size of the *second macule* which is formed discally in the same way as the first was formed subterminally. In some interspaces the number of which varies in the Lycænidæ, a proximal wedge still remains, even after the termination of the second process. At this point it may not have sufficient strength to extend again but a certain concentration of fuscous does occur, with the formation of a half halo distally, (see *halo*), this gusset-like macule appearing to the eye as a sessile *third macule* ready to emerge completely and creep in the wake of the second one. However, in certain interspaces a third wave of fuscous may extend as freely as it had done in the second process and a third macule is formed more or less dis-

Explanation of Plate V

Disposition of pigmented wing-markings in average *Lycæides*

FOREWING

From base of interspace	Macule (second)	Stretch (II–I)	Semimacule (inner first)	Interval I with aurora	Præterminal mark (outer first)	Terminal space	Terminal line	Termination of vein
83–142	R_4 142–152	152–168	R_4 168–170	170–186 (170–172)	R_4 186–190	190–198	R_4 198–200	R_4 at 190
100–144	M_1 144–153	153–170	M_1 170–172	172–187 (172–175)	M_1 187–193	193–198	M_1 198–200	M_1 at 200
100–138	M_2 138–149	149–166	M_2 166–168	168–183 (168–174)	M_2 183–189	189–193	M_2 193–195	M_2 at 197
80–128	M_3 128–139	139–158	M_3 158–161	161–176 (161–173)	M_3 176–184	184–188	M_3 188–190	M_3 at 191
48–111	Cu_1 111–126	126–151	Cu_1 151–154	154–168 (154–168)	Cu_1 168–176	176–181	Cu_1 181–183	Cu_1 at 185
0–116	Cu_2 116–123	123–144	Cu_2 144–146	146–157 (146–151)	Cu_2 157–163	163–173	Cu_2 173–175	Cu_2 at 175
0–116	1A 116–123	123–143	1A 143–145	145–156 (145–148)	1A 156–160	160–166	1A 166–168	1A at 170

Other macules: First discoidal RM (= 10 scale lines, on 100); Lateral macule R_2 (= 5 scale lines, on 125); Second macule R_3 (= 4 scale lines, on 145); First macule R_3 (evanescent).

HINDWING

0–55	Sc 55–65	65–92	Sc 92–97	97–112	Sc 112–117	117–129	Sc 129–130	Sc at 105
31–84	Rs 84–93	93–110	Rs 110–115	115–131	Rs 131–141	141–148	Rs 148–150	Rs at 140
57–97	M_1 97–105	105–122	M_1 122–127	127–145	M_1 145–155	155–160	M_1 160–162	M_1 at 155
57–96	M_2 96–104	104–124	M_2 124–130	130–141	M_2 141–154	154–160	M_2 160–163	M_2 at 163
48–86	M_3 86–93	93–115	M_3 115–120	120–133	M_3 133–147	147–155	M_3 155–157	M_3 at 158
30–76	Cu_1 76–84	84–105	Cu_1 105–112	112–130	Cu_1 130–143	143–147	Cu_1 147–150	Cu_1 at 151
0–87	Cu_2 87–93	93–104	Cu_2 104–109	109–120	Cu_2 120–129	129–139	Cu_2 140–143	Cu_2 at 145
0–88	1A 88–93	93–102	1A 102–107	107–118	1A 118–127	127–133	1A 133–136	1A at 140
0–77	2A 77–82	82–98	2A 98–103	103–112	2A 112–120	120–124	2A 124–125	2A at 130

Other macules: Third in Sc (19–27); Third in Cu_2 (37–43); One in 4A (43–46); First RM (= 5 scale lines, on 57); Second (R) M (= 6 scale lines, on 32).

Explanation of Plate V

Disposition of pigmented wing-markings in average *Lycæides*

FOREWING

From base of interspace	Macule (second)	Stretch (II–I)	Semimacule (inner first)	Interval I with aurora	Præterminal mark (outer first)	Terminal space	Terminal line	Termination of vein
83–142	R_4 142–152	152–168	R_4 168–170	170–186 (170–172)	R_4 186–190	190–198	R_4 198–200	R_4 at 190
100–144	M_1 144–153	153–170	M_1 170–172	172–187 (172–175)	M_1 187–193	193–198	M_1 198–200	M_1 at 200
100–138	M_2 138–149	149–166	M_2 166–168	168–183 (168–174)	M_2 183–189	189–193	M_2 193–195	M_2 at 197
80–128	M_3 128–139	139–158	M_3 158–161	161–176 (161–173)	M_3 176–184	184–188	M_3 188–190	M_3 at 191
48–111	Cu_1 111–126	126–151	Cu_1 151–154	154–168 (154–168)	Cu_1 168–176	176–181	Cu_1 181–183	Cu_1 at 185
0–116	Cu_2 116–123	123–144	Cu_2 144–146	146–157 (146–151)	Cu_2 157–163	163–173	Cu_2 173–175	Cu_2 at 175
0–116	1A 116–123	123–143	1A 143–145	145–156 (145–148)	1A 156–160	160–166	1A 166–168	1A at 170

Other macules: First discoidal RM (= 10 scale lines, on 100); Lateral macule R_2 (= 5 scale lines, on 125); Second macule R_3 (= 4 scale lines, on 145); First macule R_3 (evanescent).

HINDWING

From base of interspace	Macule (second)	Stretch (II–I)	Semimacule (inner first)	Interval I with aurora	Præterminal mark (outer first)	Terminal space	Terminal line	Termination of vein
0–55	Sc 55–65	65–92	Sc 92–97	97–112	Sc 112–117	117–129	Sc 129–130	Sc at 105
31–84	Rs 84–93	93–110	Rs 110–115	115–131	Rs 131–141	141–148	Rs 148–150	Rs at 140
57–97	M_1 97–105	105–122	M_1 122–127	127–145	M_1 145–155	155–160	M_1 160–162	M_1 at 155
57–96	M_2 96–104	104–124	M_2 124–130	130–141	M_2 141–154	154–160	M_2 160–163	M_2 at 163
48–86	M_3 86–93	93–115	M_3 115–120	120–133	M_3 133–147	147–155	M_3 155–157	M_3 at 158
30–76	Cu_1 76–84	84–105	Cu_1 105–112	112–130	Cu_1 130–143	143–147	Cu_1 147–150	Cu_1 at 151
0–87	Cu_2 87–93	93–104	Cu_2 104–109	109–120	Cu_2 120–129	129–139	Cu_2 140–143	Cu_2 at 145
0–88	1A 88–93	93–102	1A 102–107	107–118	1A 118–127	127–133	1A 133–136	1A at 140
0–77	2A 77–82	82–98	2A 98–103	103–112	2A 112–120	120–124	2A 124–125	2A at 130

Other macules: Third in Sc (19–27); Third in Cu_2 (37–43); One in 4A (43–46); First RM (= 5 scale lines, on 57); Second (R) M (= 6 scale lines, on 32).

cally. The occurrence of yet a fourth process has been noted only in a limited number of forms (*e.g.* in the Lycænidæ like patterns of certain Riodinidæ).

Having retained a certain vitality even after it has been formed (or owing to an extension of the wing membrane in the termen) the first macule splits, *i.e.*, the distal part stretches and snaps off and then a fissure is formed, within which very often the neutral ground undergoes an auroral andor structural differentiation. In certain species where the general process started very early (*e.g.* in *Tomares*) a splitting occurs too in the second macule of the interspace (and the resulting fissure is also differentiated aurorally from the ground, or, *e.g.* in *Cosmolyce boeticus* Linn. (*Catochrysopinæ*) is filled with white structural scales).

Thus the difference we see in the position of the same macule when comparing two specimens is really a matter of different limits attained by the sequence of initial rays. In comparing specimens, however, the eye sees those differences as the result of the actual "movement" of this or that macule distad and this is a true impression, inasmuch as a macule is formed at different limits of the distally progressing infuscations. On the other hand, the white cretule capping a semimacule proximally (and produced not only by a gradual draining of the ground on the part of the first macule but also by the force of the stretch attending the splitting of the latter), is not at all "growing basad" as one is tempted to see it in some forms: in direction of growth and in shape it adheres to the general standard, for it should be noted that the essential shape of a macule and its halo, of a semimacule and its cretule, of an interval and its aurora, of a præterminal mark and its scintilla, is obovate, sagittate, cordate, arcuate, with the wider part directed distad; this outline repeats that of a sessile macule which in its turn conforms to the shape of the apex of the cell; or in other words, the shape of any of these markings renders macrocosmically the shape of each distally broadening scale and microcosmically the general fanwise expansion of the wing and its cells, and is influenced in details of outline and direction by the apical andor cubito-anal development of the termen (alone the ciliary markings, lying as they do beyond the membrane of the wing, point distad). I see no trace or possibility of the basally directed development of markings postulated by authors to explain certain phenomena of pattern.

Pseudo-linear arrangements of markings, insofar as they occur in the Lycænidæ, must be also briefly noted. The terminal line is the only sequence of interspatial markings for which I employ the word "line" at all, as it is the simplest term. Although it may be the remaining maximal limit of an infuscation preceding the formation of the first macule, its connection with ciliary elements places it in a separate class (submarkings) from the macules. It would not have mattered much had I called it "limbal" with Herrich Schäffer or "extreme" with Schröder, or "marginal" with the British authors. But if I called it "Line I" with Eimer (who has eleven of them numbered basad) or "XII" with Verity (who has twelve of them, numbered distad), or "22d" with Kusnezov (who has twenty-two) or "external I" with Schwanwitsch (who has three such external ones) or "Randbinde I" with Süffert (who has two such "Randbinden"), then I would be instantly involved in a wild confusion of man-made patterns. I fail to perceive in the Lycænid wing any suggestion whatsoever of initial transverse lines or stripes forming, or having formed, an integral part of the pattern and lending themselves to classification and "homologisation." In Lepidoptera generally, the limit of a lost ancestral infuscation in any place within a given cell, may produce, in combination with a similar limit occurring at more or less the same point in an adjacent cell, what may be loosely termed a line. When this occurs in several interspaces without a special macular differentiation in any, and is followed by various adjustments and adaptations to the distal outline of the wing in the course of more or less synchronized stages of posterior and anterior development of the termen, then the line may seem very perfect to the eye, but it is the *result* of those processes and not a "primitive" line which Mother Nature automatically traced with her brush on one butterfly after another as soon as she had stuck on the wings.

It is never the line as such that "breaks" into ocelloid macules. Such macules are formed by the initial spread of fuscous, or not at all; and sometimes when the latter had been strong enough interneurally to span that space, the resulting macule may be broad enough to "connect" with any other macule (not necessarily of its "own," *i.e.*, synchronous series) formed in an adjacent cell; or, more seldom, during the process of concentration + draining + isolation the macule may steal additional pigment from the ground of a neighboring unoccupied interspace and form therein part of its halo.

Even in the most zebroid species of *Catochrysopinæ* or *Theclinæ*, the macules peep through their linear disguise. If on the basis of some synthetic "prototype" we tried to classify these lines (say Lx, Ly, Lz), we would be continuously mistaking proximal and distal parts of split macules for components of different linear sets, or, in other cases, would come to the nonsensical conclusion that the same macules (*e.g.*, the second macules of the posterior interspaces) form the lower part of Lx in one species, the lower part of Lz in another, and an intermediate Ly in a third. The illusion of a stripe in the subfamilies mentioned is due to several variously combined factors. The macules in two or more adjacent cells may be bar-like, with halos formed only laterally. Sessile third macules (half haloed, *i.e.*, only distally) wedged proximally in their interspaces, *e.g.*, in R_4 (just above the outer part of a split discoidal macule) and in M_3 (just between the discoidal outer portion and the second macule in Cu_1), combined with a posterior sequence of second macules in Cu_1, Cu_2, and A1 may complete the illusion of a stripe crossing the wing radianally. Moreover, when these macules are comparatively weakly pigmented, the eye tends to confuse them with portions of ground color; or a complete transverse section of brown ground between "white lines" (formed by the inversely in regard to each other directed half halos of two different macular series) may be mistaken for a "stripe." Remarkable cryptic phenomena in some genera produce yet other illusory patterns, and a "white line" that the eye follows across two cells may really consist of a proximal half-halo in one and a distal one in the other. Finally, it should be kept in mind that among the second macules *any* three may be *always* seen in line provided that two of them (such as A_1 and Cu_2 or M_1 and M_2) are those which, throughout the family, are more or less linked together in their movement distad. Although quite possibly my judgment may be affected by the fact that the genus which I have especially studied and to which we must now turn is most honestly "spotted" — and also by the fact that I am interested more in what happens within a given interspace than in the wing pattern as a whole, still I am quite sure that it would be a waste of time to try and twist this or that illusion created by a transverse combination of Lycænid macules into this or that "prototypical line."

The wing-characters of the genus Lycæides

The categories to be discussed are: I. Size and shape. II. Ground. III. Cyanic overlay. IV. Vadosal elements. V. Scintillant elements. VI. Hairscales. VII. Terminal submarkings. VIII. Maculation. (Number of specimens of *Lycæides* forms examined: 959).

I. Size and Shape.

Length of forewing (from base of Cu to end of M_1) in smallest individual measured: 7.5 mm., with length of hindwing (from base of Cu to end of M_2): 6.5 mm.; in largest individual measured these lengths are: 18.5 and 15 mm. respectively, thus giving a range of 11 mm. and 8.5 mm. Number of scale lines ranging from 140 in forewing and 115 in hindwing to 260 and 210 respectively. In average sized forms the number of scale lines varies from 190 to 210 in the forewing and from 160 to 170 in the hindwing. The hindwing varies less than the forewing in the number of scale lines but more in shape. The most distal point of the termen of the hindwing lies either rather anteriorly (*high angled* shape), namely between M_1 and M_2, or more posteriorly (*low angled* shape), between M_2 and M_3, or rather exactly at the end of M_2 (*average* shape); or the termen is evenly rounded, *i.e.*, runs almost concentrically to the scale lines in the stretch from M_1 to Cu_1 this however only occurring in stunted individuals. In especially high-angle individuals the scale line which in the hindwing coincides with the tip of Cu_1 (further on termed s.l.Cu_1) abuts anteriorly at the tip of Rs and cuts off a terminal segment of about 20 scale lines at the point of its greatest expanse (in interspace M_2); but another individual with the same number of scale lines in M_2 will seem less conspicuously angled if s.l.Cu_1 reaches anteriorly a more distal point (say, between Rs and M_1) since the segment cut off by the line will occupy a lesser number of scale lines. In low-angled forms s.l.Cu_1 may abut at M_1, thus cutting off the terminal parts of only two interspaces instead of four. Finally the segment itself may be either of a fuller or more apical shape, and when this difference exists the wing of one individual may look rounded and that of another angular though actually both are high-angled (the tips of Cu_1 and Rs being connected by the same scale line in both). In the *circular* shapes, found in stunted specimens, sc.l.Cu_1 abuts at M_2, practically coinciding with the termen and thus cutting off no segment at all. In the forewing the variations are less conspicuous but there is generally some correspondence between the wings since in high-angled forms the forewing is apt to be "pointed," *i.e.*, with the scale line which connects the tips of M_3 and R_4 cutting off a larger segment (about ten scale lines in a "rounded" forewing and about twenty in a "pointed" one). *Short* forewings (where the proportion between breadth and length is less than five to four) and *long* forewings (when more than five to four) may have, together with difference in shape, a certain significance in subspecific values. It may be added that there is a certain connection between shape (*i.e.* vigor of growth in termen) and color (vigor of pigmentation). A low-angled shape is generally associated with weakly pigmented undersides, and these are generally strongly pigmented in races with high-angled hindwings.

II. Ground.

Upperside, both sexes: ranging from neutral fuscous or weak brown to blackish. Costa in hindwing above Sc of a scaly neutral fuscous still weakened by the addition of colorless or very faintly iridescent scales. In a few female forms, with greatly developed upperside auroræ (see VIII 4), the fuscous ground may be intermixed with sparse auroral scales (the beginning of a brightening of the ground which in both sexes of *Plebulina* is well on the way to complete predominance, as occurring in *Lycæninæ*).

Underside, both sexes: ranging from fawn to brownish; or from white (colorless scales completely covering some, or all, neutral ground areas) to whitish fawn; or producing a greyish or bluish effect due to the even admixture of colorless or faintly iridescent scales with a more or less developed ground pigmentation. Occasionally the veins and the vein scars appear marked in a lighter shade. The forewing is generally of a slightly more diluted and smoother tone than the hindwing, and in one and same race the ground of the female is generally slightly richer than that of the male.

III. Cyanic overlay.

Upperside, both sexes: structural scales invading the ground from the base with more or less vivid violet blue; partly (a) or almost completely (b); (a) clothing or dusting only certain areas (*i.e.*, absent discally, or only empurpling the cretules (*q. v.*) in the female) or reduced to a few scales at the base; (b) overlaying the ground evenly or more or less sparsely (*i.e.*, leaving out minute bald patches and the vadosal elements, *q.v.*) but always keeping clear of the costa in both wings, of most of the subcostal area in the hindwing (see further, V, 1 and IV, 5, 6) and reaching distad a maximum limit situated at a distance of about three scale-lines from the termen (see IV, 4) and less sharply defined in the female than in the corresponding male; the intensity and tint of the violet blue depending upon the density of the scaling producing it, as well as upon the fundamental pigmentation of the wings.[10] Reduced or absent in the female considerably more often than in the male, where its complete absence occurs only in a few races.

IV. Vadosal elements.

Racially more or less characteristic portions of fuscous upperside ground inasmuch as they are isolated, defined, and strongly pigmented in forms (mainly male) with dense cyanic overlay which in its spread distad leaves "dry" or fails to reach always three (fourth, fifth, and most of sixth), but often all of the following ten ground elements: the (1) *vadosa* proper: a longitudinal stretch of ground thickly or finely sheathing a vein throughout its course (or only terminally: (2) *terminal vadosa*), often broadening towards its tip (on veins R_4 /Rs/ down to 1A) to form there the basally tapering (3) *vadosal triangle* (in shape and position a more or less exaggerated silhouette of the corresponding inner triangle *q.v.* of the underside) which may occur independently and which in its turn fuses with (and rep-

[10] Culling at random definitions of these shades from original descriptions of *Lycæides* forms, I find: dull violet, shiny blue, glossy violet blue, silky lilac blue, deep purple, hyssop violet, lavender blue, pruinose blue, pinky lilac, violet with a pink tinge, and at least two authors have found in their races a greenish cast. All these, more or less subjective, color impressions are worthless as racial characters unless the combination of the two factors producing the color effect (in fresh specimens) be carefully analyzed in comparison with fresh specimens of other races (of the same and of different species).

resents the neural thickening of) the (4) *vadum.*[11] a linear or more extensive marginal space of pigmented ground, from apex to tornus, between the limbal limit of the overlay and the termen, at its narrowest reproducing the terminal line of the underside, apically turning into the delicate (5) *costal vadum* of the forewing, merging with the distally fuscous Sc area ((6) *subcostal vadum*) of the hindwing, distally connected with the vadosal fringe *q.v.*, and with the outer triangles *q.v.* and proximally (in the hindwing) often joined more or less thickly by means of an (7) *interneural vadosa* with the (8) *insula* proper (as differing from (9) *insula Rs II* and (10) *insula RM*) which is a frequently occurring, more or less isolated, roundish blotch or point of conspicuous fuscous repeating in all or some interspaces the corresponding præterminal mark *q.v.* of the underside (also, but usually faintly, macule Rs II, and in some cases, mainly in females with strong overlay and mainly in forewing, macule RM), and sometimes appearing as a blacker spot within the vadum when the latter is extensive enough to surround it, but not sufficiently dark to merge with its pigmentation.

V. Scintillant elements.

1. The *scintillant pulvis*: structural scales more or less extensively dusting with metallic greenish blue (in strongly pigmented forms) or turquoise (in weakly pigmented or white forms) the ground at the base and in the anal interspaces of the underside; mainly in hindwing; sometimes quite absent or reduced to a few scales next to the body. Upperside: confined to the dorsum and to the proximal and posterior part of the subcostal interspace of the hindwing and intergrading there with the main overlay; in a few female forms, occurring also on the upperside of the forewing where it clothes the costa and lines the veins discally (*i.e.*, more or less corresponding to the distribution of short white hairscales in the male); consisting there of rather coarse scales of a dull turquoise tone suggesting "dead" parts of the cyanic overlay.

2. The *scintilla*: [12] a variable number of scintillant scales more or less thickly and evenly grouped, overlaying the pigment

[11] "fuscous border," "bordure noire," "Distal Rand," "terminal border," "kraievaya polosa," "marginal streak," etc., of authors.

[12] Possibly remnants of a dense scintillant pulvis which had covered the whole of the hindwing, completely swamping all its markings, at some period in the evolution of the Lycænidæ, as it still does in certain Asiatic species of *Albulina*,

of each præterminal mark of hindwing underside; tending to be gradually reduced from M_3 or M_2 costad, and often lacking in the anterior interspaces, but seldom missing in the posterior ones; very poorly developed in some forms but only individually quite absent; in most cases placed rather proximally upon the mark, *i.e.*, not reaching its distal limit, so that the latter spreads out beardlike from underneath the scintillant incrustation, if viewed from the termen; (the following more individual than racial variations in position are to be noted since any one of them can be stabilized specifically in other genera) sometimes coming in complete contact with the aurora (*q.v.*), but often well separated from it by a tendency to occupy a median, or even distal, position within the mark; sometimes absent from a more or less conspicuous point in the center (upon the interneural fold) which thus forms a blackish pupil; in some cases agglomerating band-like across the mark; or distributed unevenly, with patches and dots of black showing at different points; but in a few cases overlaying the mark completely (with or without a pupil), or, as it were, overlapping or replacing it in cases when the pigment of the mark tends to obsolescence or is quite gone; in shade varying (racially, inasmuch as the pigmentation varies racially) to the naked eye from turquoise (in poorly pigmented forms) through peacock blue (at an average or reduced development in well-pigmented forms) to golden green (when completely overlaying a strongly pigmented mark), but hardly distinguishable from the scintillant pulvis under lens (both sets of scales being turquoise), the aforesaid variations in color depending on the angle of light, the compactness of scales, the pigmental basis and frame — and a subjective approach on the part of the observer.

VI. Hairscales (and androconial scales)

1. *Hairscales* of forewing, in male: very short, white, bluish, or pale violet blue (according to light); of a bristly appearance under lens; projecting distad (apically and tornad when paired on a radial vein, on each of which they may form a sequence of basally pointed arrowheads) and sparsely to rather densely distributed (more or less distally) within cell RM and throughout the circumcellular area distad, lacking at the base of its posterior

Glaucopsyche, *Lycæna*, and *Tomares*, and which subsequently had disappeared, leaving the scintillæ as seapools are left by the sea at low tide.

part, stopping or diminishing in number at or beyond limit II (*i.e.* the limit corresponding to the emplacement of second macules, *q.v.*, of the underside) but sometimes just reaching in hindwing (where however they are somewhat less conspicuous throughout than in the forewing) limit I (*i.e.*, the limit corresponding to the emplacement of the semimacules *q.v.* of the underside). Above RM in forewing mainly along veins Sc, R_1, R_2, and R_3, agglomerating on their slopes (giving the vein a pinnate appearance) when the overlay is dense enough to eliminate the vadosæ in the costal area which then seems, especially in freshly emerged specimens, rather densely powdered with white (*costal pulvis*).

2. *Male androconial scales*: a microscopical character: minute battledore-shaped scales, in outline, size, length of pedicule and number and density of "knots" varying in individuals of some forms, racially more or less constant in others (especially in stunted or overdeveloped forms), and often duplicated by specifically different races (and thus lacking the specific importance assigned them by Courvoisier, 1917, on the strength of scanty, and more or less misidentified, European material).

3. *Costal fringe:* short hairscales (allied to the male hairscales) in both sexes rimming the costa with white and very conspicuous in specimens with a strongly pigmented costal vadum (IV, 5).

4. *Basal cilia:* long and very long silvery white, bluish or drab hairscales clothing basally the upperside of the hindwing (reduced in forewing), sweeping in a distal and then downward direction across the proximal part of cell RM, extending rather far into interspace Cu_1 where they just reach limit II, still further in Cu_2 + 1A (almost to limit I), and spreading from base into 2A and 4A, where they stipple the scintillant pulvis of the dorsum.

5. *Dorsal cilia:* white, or producing on the upperside a light blue effect as if daintily dyed. Springing from a very faintly fuscous *dorsal margin* and sometimes slightly infuscated themselves. Equal to about 10 s.l., somewhat shorter in forewing.

6. *Terminal cilia* as seen from the underside: long hairscales (equal to about 10 s.l. in forewing and to 12 s.l. in hindwing) attached to the termen, proximally denser than distally; silvery white or with slight bluish or mother-of-pearl reflections in certain lights; sometimes, especially in females, more or less

infuscated, ranging in shade from drab or pale fawn to brownish; completely pigmented or in part, *i.e.*, only proximally or only distally and then either from tornus to apex throughout, or only along a limited section of that range.

7. *Vadosal fringe:* consisting of rather short pigmented hairscales rooted in the vadum, upperside, and thus doubling basally the terminal cilia of the underside; usually equal to 4 s.l.; tending towards the fuscous of the vadum from which sometimes it may be almost indistinguishable to the naked eye.

Viewed in cross-section the short dark vadosal fringe (rooted in the still darker vadum) is seen to overlay the long white underside cilia (rooted in the distal edge of the terminal line) to about 2/5 of their length. The very slight jutting of the dark hairscales of the terminal line just beyond the rim of the membrane forms a kind of prop for the base of the ciliary hairs which thus are encased between it and the vadosal fringe. If the cilia are viewed from the under surface by the naked eye, an illusory more or less dark ciliary line seems to run along the middle of their transverse stretch: this is due, first, to the cilia abruptly losing their quilted appearance at 2/5 of their length where the edge of the upperside vadosal fringe stops, and second, to minute portions of this edge being discernible in between the white ciliary hairs, as they become less dense distally. If, moreover, the distal part of the cilia on the underside happens to be infuscated and if this infuscation begins at just over 2/5 of the length distad, then on the upperside too there is a similar illusion of a ciliary line (but of a light one this time), due to a narrow stretch of unpigmented cilia showing between the distal infuscation and the edge of the dark vadosal fringe which shuts off most of the white basal part of the underside cilia. My abundant material has not proved the occurrence of a true ciliary line in *Lycæides*, *i.e.*, of an actual infuscation of each ciliary hair only at its middle, or of shorter hairs (among the longer ones) infuscated only at the very tips.

VII. Terminal submarkings of underside.

1. The *terminal line:* edging the termen proximally with more or less dense fuscous from about the middle of i.Sc. in secondaries, and from the tip of R_4 in primaries, to the tornus; consisting of very short distally directed hairscales (which very slightly jut beyond the termen), and in its interspatial aspect

resembling a garland more or less raised and thickened at both ends. Very thin and faint in weakly pigmented form.

2. The *inner triangle:* a fuscous triangular basally tapering mark formed upon the termination of each vein (mainly from M_1 to Cu_2) by the meeting of the thickened præneural ends of two adjacent sections of the terminal line. Not necessarily absent in weakly pigmented forms. See also IV, 3.

3. The *outer triangle:* a fuscous subtriangular distally tapering mark formed upon the proximal part of the terminal cilia (and also occurring sometimes upon the vadosal fringe of the upper side) independently from the general pigmentation, if any, of the latter and placed directly opposite (base to base) the inner (or the vadosal) triangle, which it repeats in reverse, except that its base is usually narrower and its point more or less truncated. Mainly in hindwing. Seldom leading to any conspicuous scuttelation in the forewing.

VIII. Maculation of underside.

Counting from termen basad a *first macule* (split into inner and outer part) and a *second macule* are both represented in Sc., Rs, and 2A of hindwing, in R_3 (where, however, they occur seldom and are always much reduced) and R_4 of forewing, and in M_1, M_2, M_3, Cu_1, Cu_2, and 1A (small in the two last) of both wings. A *third macule* supplements the set in Sc and Cu_2 of hindwing. Moreover, there is a small *lateral macule* in 4A of hindwing caught in the blind alley of the dorsum and sometimes a small lateral macule is somewhat similarly trapped in R_2 of forewing (where the eye sees it as "belonging" to the transverse series of second macules). In both wings the discoidal cell (a double interspace R and M) has its own *first* (double) *discoidal macule,*[13] the rheniform RM, traversed by the discales (the outer segment of its R part and the outer segment of its M part form in relation to the second macules M_1 and M_2 a pair of sessile third macules — an important point in the case of certain other genera). In the hindwing there is a *second* (single) *discoidal macule* within the cell under the scar of vein M. All the macules are of a more or less deep fuscous and are rimmed with structural scales, *i.e.*, *halos* (produced by the macule having drained during its period of formation and concentration the initial pig-

[13] Among the names employed by authors for this double macule are "discal streak," "bar," and "disco-cellular lunule."

ment in its immediate neighborhood). The halves of the halo which has split together with each first macule are termed *cretules* but only the proximal one is represented in full. The inner part of each first macule is the *semimacule* (capped or rimmed proximally by the cretule) and the outer part is the *præterminal mark* (adorned in hindwing with the scintilla). The fissure between the two parts is the *interval* (extending in average size races from about 5 to 20 scale lines in Cu_1 of forewing, always correspondingly more in hindwing) which may be, and generally is, more or less completely filled by the *auroral element* — an agglomeration of brightly colored scales differentiated from the ground, and associated with the splitting of macules. In the female the semimacules and præterminal marks may appear in darker pigment within the fuscous ground of the upperside, and the series of *auroræ* is often repeated, completely or in part; but in the males with average overlay only the præterminal marks appear (as *insulæ*) although in very rare aberrations the posterior auroræ of hindwing may be repeated (as happens more often in forms of *Plebejus argus* L., becomes fairly normal in its allies and is characteristic of the smaller *Icaricia* where the auroral development resembles that found in certain *Glaucopsychinæ*). All parts of the first macule are less developed in the forewing than in the hindwing, where again those in M_3 and especially Cu_1 (there extremely developed in "tailed" genera) are stronger than in the rest of the interspaces.

VIIIa. Elements of First Macule.

1. *Semimacule:* [14] generally crescentic, sagittate, or deltoid (pointing basad upon the interneural fold) in hindwing (from i.Sc to A_2 incl.); when well developed, spanning almost the whole breadth of the interspace, except in Sc, Rs, and M_1, where it is shorter and often reduced to an uneven bar-like shape; often tending to the latter shape in all interspaces of forewing (from i.R_4 to i.1A incl.) where each is shorter than the corresponding one of the hindwing and may seem blurred to the naked eye owing to a weaker pigmentation. Variable in longitudinal extension; quite absent only in extreme individuals of very weakly pigmented races.

[14] The "rather narrow bent lunule" of Scudder and the "crescent," "flat crescent," "arrowhead," and "chevron" of Chapman; those two authors have left by far the best descriptions of the Lycæides pattern.

2. *Cretule:* capping proximally each semimacule in both wings; more or less conspicuously white or whitish (almost invisible on the powdery white ground of some forms) or, very rarely, retaining some diffuse pigment; crescentic or sagittate or squarish, *i.e.*, more or less in keeping with the shape and size of the corresponding semimacule, but usually somewhat more pointed and larger; sometimes so greatly developed as to seem to fuse with the halo of the corresponding second macule (actually it is the halo which intrudes), and then appearing raylike if the whole system of macule I is transversally reduced; at other times, however, especially in hindwing where the semimacules are better developed, and more often in females, occupying the whole breadth of the interspace for a certain distance basad from semimacule before "terminating" crescentically or tapering to a point (phylogenetically, however, expanding distad from that point), so that the sequence of cretules (especially if they fuse with the halos of series II) has been described by observers as a "white band"; in some well pigmented forms very small or quite absent, especially in forewing. Appearing on the upperside in some females, in whitish or bluish (or violet as portions of the overlay).

3. The *prœterminal mark:* tending to be heart-shaped (expanding distad) in hindwing where it is generally strongly fuscous and contains the scintilla; roughly rhomboidal or (when reduced) bar-like in forewing where its pigmentation is weaker; situated in the same interspaces as the semimacule distally to the latter, and varying in size accordingly; tending to complete obsolescence in some weakly pigmented forms, although the scintilla may be retained (see V,2).

4. (The remnants of an) *outer cretule:* colorless (white) scales diffused in the ground of the crescentic terminal space with which, when the latter lacks pigment altogether, it is practically synonymous; usually more conspicuously white in hindwing but sometimes very much so in Cu_2 of forewing in otherwise well pigmented forms. Appearing on the upperside in some females with the same variations as 2.

5. The *aurora:* racially varying in extension (together with that of the interval) and in transversal development, (together with that of the semimacule); on the underside in both sexes(but somewhat better developed in the female); ranging there from light yellowish to deep reddish orange; of

a more velvety appearance on the upperside of the female where it may be under or overdeveloped in comparison to the underside in the same specimen and where its color ranges from a bleached neutral shade to a rich fulvous (the slight discrepancy in tone between the two surfaces being due to a difference in the degree of the ground pigmentation as well as to the sparser spread of colored scales forming the average upperside aurora); at its full development on the underside snugly fitting into the interval between the semimacule which caps it and the corresponding præterminal mark which it caps in its turn; often represented in all intervals; tending, however, to be ill-formed, underdeveloped, or absent in the primaries, especially in R_4, M_1, M_2, Cu_2, and A_1 (termed the *weak interspaces*) of the male underside and of the female upperside; in a few female forms, however, hypertrophied on the upperside and especially conspicuously so in the forewing, the sequence reaching there from costa to dorsum and swamping a stretch corresponding to that occupied on the underside by the inner cretule + semimacule + aurora, thus forming a broad "band" with a more or less diffuse proximal edge (see also II); when underdeveloped the aurora edges the interval always proximally, *i.e.*, does not reach the præterminal mark in its growth distad from "beneath" the semimacule (the remaining gap being either concolorous with the ground or colorless). It is the first to develop, or the last to go, in Cu_1 (with its neighbor in M_3 following closely). Completely absent only in extreme individuals of weakly pigmented forms.

5a. *Cusps:* when fully developed and especially in Cu_1 and M_3 of the hindwing underside, the crescent of the aurora is prolonged distad by two (inner and outer) pairs of cusps and occupies the whole breadth of the interspace; the inner cusp clasps the præterminal mark laterally, the outer one runs next to the vein and fuses upon the vein with the outer cusp of the adjacent aurora to finally penetrate and bisect the inner triangle of the terminal line; in the forewing and in the anterior interspaces of the hindwing the outer cusp tends to be absent, so that the auroræ (and their semimacules) do not touch the veins and are separate from each other.

5b. *Lacrimæ:* in some richly pigmented and strongly developed forms there are on the underside two or four streamlets of blurred auroral pigment coming as it were from beneath the præterminal mark, and "trickling" distad across the terminal space (one, or a pair, on each side of the interneural fold).

VIIIb. Second, Third, Discoidal, and Lateral Macules.

Second macules: if a *Lycæides* forewing is placed with its base towards the observer and its discal constellation is viewed from an imaginary horizontal line joining the opposite ends of the discales, the *second macules*, (R_3), R_4, M_1, M_2, M_3, and Cu_1 [15] all of which have radiated from positions adjacent to cell RM, are seen to form a fairly regular rather weak arc, sloping somewhat sideways in relation to the rheniform macule RM, as if tipped by a slight apical pull (process 3). The twin macules Cu_2 and 1A lie outside the lower end of the arc, *i.e.*, lead an independent existence, having reached their present position (phylogenetically, from an enormously remote starting point in comparison to the starting points of the other macules) in result of a (process 2) cubito-anal stretch of the membrane (so conspicuously retained in some genera) that had occurred at some period in the evolution of the narrow and ovoid ancestral forewing (with a similarly shaped hindwing) prior to the comparatively recent generic and tribal apical development (process 3) which in a way has tended to repeat the initial growth and elongation of the ancestral wing (process 1). These stages of unequal growth and of subsequent compensatory readjustment may be compared to the already discussed evolutionary phenomena in the case of the uncus.

It would be necessary to analyze a great number of generic patterns (in the *Plebejinæ* alone striking variations on a P-shaped basis occur in *Agriades*, and a remarkable apicoid angle is formed by the macular constellation in *Albulina*) in order to bring out certain features of the position of second macules in *Lycæides*, but this would transcend the scope of this paper. In selecting the three positions (1 proximal, 2 central, and 3 distal) given for this genus, stress has been laid on the progress of macule Cu_1, but actually this may be combined, at these and intermediate stages, with shiftings on the part of the anterior series which may be removed from RM further than it is shown here. Fig. 2a shows the generic starting point of R_4 whose initial rather distal position (in regard to even such

[15] When no Roman number is appended to the symbol of the macule, the reference is to the second macule (e.g. $Cu_1 = Cu_1$ II).

genera in *Plebejinæ* where the constellation is of the same type) coupled with the also rather distal position of R_2 or R_3, when occurring (not shown in the figures), is instrumental in weakening the curvature of the arc and producing its "sideways" position already discussed. The same figure also shows the most proximal position of macule Cu_1 which is at this stage in an oblique line (the *radianal slant*, reoccurring throughout the family) with RM and $Cu_2 + 1A$. Under RM this imaginary line diverges distad from the latter's scale line to finally cross the scale-line of macule Cu_2. Fig. 2b shows a middle position which is most frequently found in this genus. Fig. 2c shows the most distal position of Cu_1 (except that the whole series can move still further if the semimacules are further removed than they are in average forms) when the series is roughly adapted to the sequence of the first macules which in its turn is subparallel to the outline of the termen. The tendency to assume one of the two extreme positions (a, b) is sometimes a racial character.

In forewings of average extension (about 200 s.l. in M_1 and 185 in Cu_1) and with semimacule Cu_1 having reached s.l. 150 or thereabouts, the range of movement of the center of macule Cu_1 (and it is this center which is referred to throughout), is from s.l. 105, at which initial point in *Lycæides* it is about 50 s.l. removed from the apex of its cell (which thus is less than macule R_4 has travelled from the apex of cell R_4 but *more* than the distance covered by the other anterior macules in regard to their respective cells — although curiously enough all describers, being obsessed by the notion that macules must form "lines," speak of Cu_1 in this position as "advanced basally") to s.l. 135, at which point it has 50 scale lines to go if it wishes to reach the termen, which of course it cannot, since the split first macule occupies the remaining space. Thus its range of activity is 30 s.l. which is somewhat less than 1/4 of the length of its interspace and about 2/5 of the distance from the proximal position of Cu_1 to the termen (this range varies racially). The width of the interval between semimacule (inner I) and præterminal mark (outer I) (see fig. 2d, e, f) is mainly dependent on the position which the former had reached when the macule I split (the outer part wandering distad). The breadth of the fissure (interval I) ranges from 4 s.l. to at least 20 (average sized males). The space available for the progress of macule Cu_1

depends on the position reached by the center of the corresponding semimacule (this is about s.l. 145, proximal limit, about 155, average, and about 165, distal). Thus when the latter reaches its distal limit (resulting in a narrow interval I, since the præterminal mark cannot wander away beyond a certain limit), the increase in the II–I stretch allows macule Cu_1 a

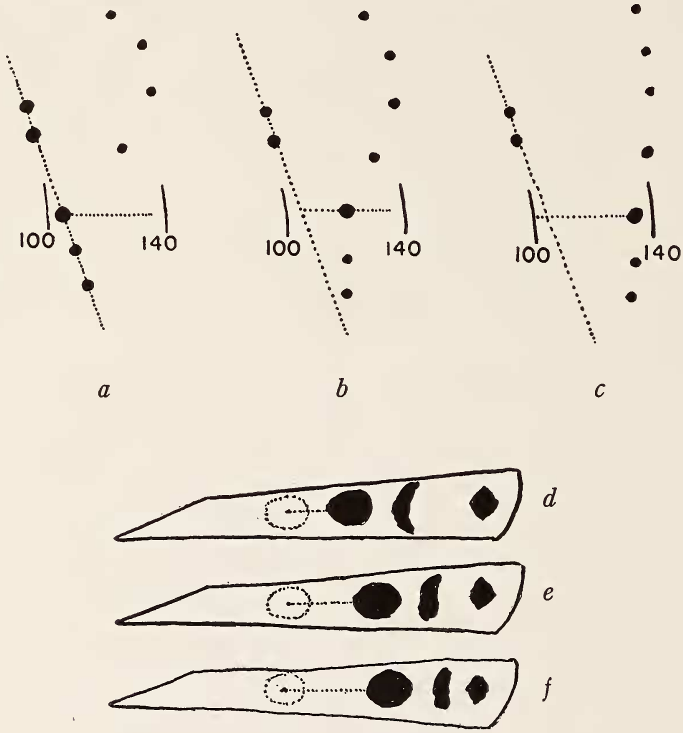


FIG. 2. a, b, c, Forewing discal constellation in *Lycæides*, showing proximal, central and distal position of second macule Cu_1. d, e, f, Cell Cu_1 of forewing, showing relation in position between semimacule (inner part of first macule) and second macule.

greater range (at least 40 s.l.). A terminal extension of the wing even to only 195 in Cu_1 may produce a veritable wilderness for Cu_1 to traverse. These phenomena have great racial importance.

In the hindwing the position of macule Cu_1 varies less conspicuously. The same discal arc as in forewing is readily perceived, but the eye sees Rs in a more proximal position in relation to M_1 than R_4 appears in relation to M_1 in the forewing (actually, both Rs and R_4 — especially the latter — have progressed further *distad* from their apices than the corresponding macules M_1 have progressed in their cells). Macules ScIII and ScII at one end and Cu_2 II at the other prolong the discal arc (Rs, M_1, M_2, M_3, Cu_1) in such a way as to form a horseshoe arrangement around cell RM: this *circumcellular arc* becomes practically a circle in some genera, where the second macule in cell RM (or a third one) is placed basally enough to act as a link. Posteriorly to this, macules Cu_2 + 1A, 2A and 4A form a short weak additional arc or *parenthesis* (also a special feature in certain other genera) with its concavity toward the proximal stretch of vein Cu. The radianal slant connects macules ScIII, RM, Cu_1 (when lagging) the colon (its 1A part, however, generally "diverges basad") and the semimacule in 2A by a regular but perfectly imaginary line, traversing the wing and very conspicuous and perfect in butterflies where the anal part of the termen has been stretched tailwise.

When examining *Lycœnidœ* patterns for systematic purposes, loose impressionistic descriptions will inevitably result (and I have erred myself in this respect) if the describer does not take into account the actual distances of the macules from the apices of their cells and from the termen, the actual and comparative positions of the split first macules, the extension of the split in comparison to the whole wing, the development of the terminal space, and the relation between the size of the macules and the entire number of scale-lines. I shall limit myself here to a few words regarding the dimensions of macules in this genus.

Divided by three, the sum of scale lines occupied by the three median macules II in a specimen gives pretty exactly the mean size of the whole discal maculation in that specimen. When the relation of this number to the alar expanse in scale-lines (see category I) is around 1/20 for each wing, the maculation in the specimen or in the race may be said to be of "average" development in both wings. Below this, it is "reduced"; above, it is "enlarged." In the forewing macule M_1 is often equal to M_2 but their elongation and direction may be different. R_4 is smaller than M_1 and both tend to be ovoids slanted towards the wing apex, these two being especially sensitive to the apical pull. M_2 when ovoid, tends to be slanted towards the stem of veins R_3 and R_4 just above the discoidal. M_3 when ovoid and tending towards a proximally pointed cordate shape has its axis directed anteriorly towards the discoidal and posteriorly tornad. The same is true of Cu_1 which is usually the largest in the series and is often very conspicuously elongated (in all these cases, of course, the actual extension and expansion is essentially in a distal direction). Macules Cu_2 and 1A which are often well separate and smaller than R_4 (except when the latter is very much reduced) form together a *colon*, the axis of which is directed either towards the discoidal, and appears more or less in line with the latter's axis, or towards the apex of interspace R_3 and then follows its scale-line (which is most frequently the one traversing the point of forking of veins R_3 and R_4), as the discoidal does its own, in which case, since both lie on different sections of their respective scale-lines, discoidal and colon do not appear parallel to each other, the former slanting tornad and the colon remaining "straight," *i.e.*, at right angles to the dorsum. The rare R_2 is smaller than Cu_2 (or 1A) while the slightly more frequent R_3 is scarcely perceptible to the naked eye. In a general way and disregarding the difference in elongation, the dimensional sequence of macules runs as follows: R_3, R_2, A_1, Cu_2, R_4, M_1, M_2, M_3, Cu_1, with the rheniform RM $(R + M)$ slightly broader than colon $(Cu_2 + 1A)$.

In the hindwing the macules forming the circumcellular arc are generally subequal, with Cu_2III and M_3 often tending to be smaller than the rest, while Rs tends to be slightly enlarged and ScII is still more so (sometimes vaguely suggesting a very ancient fusion of two spots in adjacent interspaces where the partition has been lost). Thus there is a gradual reduction in size from ScII to M_3 with Cu_1 subequal to M_1 and M_2. Cu_2 and 1A are the smallest in series II (and even slightly smaller than Cu_2III) and are apt to be fused forming an hour glass-shaped or rheniform (distally convex) spot not unlike the discoidal $(R + M)$ and of approximately the same size but having a different curvature of axis since they lie upon different sections of their respective scale-lines. The extension of 2A is almost that of M_2 but (transversally to the veins) it is longer and forms a roughly rheniform blotch suggesting a more complete fusion of adjacent macules in 2A and 3A (an extinct vein) than that